Commentary

Conspecific Attraction is a Missing Component in Wildlife Habitat Modeling

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ABSTRACT Wildlife biologists use knowledge about wildlife–habitat relationships to create habitat models to predict species occurrence across a landscape. Researchers attribute limitations in predictive ability of a habitat model to data deficiencies, missing parameters, error introduced by specifications of the statistical model, and natural variation. Few wildlife biologists, however, have incorporated intra- and interspecific interactions (e.g., conspecific attraction, competition, predator–prey relationships) to increase predictive accuracy of habitat models. Based on our literature review and preliminary data analysis, conspecific attraction can be a primary factor influencing habitat selection in wildlife. Conspecific attraction can lead to clustered distributions of wildlife within available habitat, reducing the predictive ability of habitat models based on vegetative and geographic parameters alone. We suggest wildlife biologists consider incorporating a parameter in habitat models for the clustered distribution of individuals within available habitat and investigate the mechanisms leading to clustered distributions of species, especially conspecific attraction. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):331–336; 2008)

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Wildlife biologists often consider habitat as a unifying concept in wildlife ecology (Morrison et al. 2006). The relationship between wildlife and the habitats they occupy has been one of the most intensively studied topics in the ecological literature (Manly et al. 2002, Morrison et al. 2006). Habitat modeling is commonly used in animal ecology to identify variables that describe a species' habitat, explain and predict species occurrence, determine available habitat for a species, and provide information for wildlife management (Mörtberg and Karlström 2005, Barry and Elith 2006). Wildlife biologists and naturalists have long described species' habitats based on vegetation and geographic characteristics (e.g., vegetation physiognomy and floristics, soil, slope, rainfall, climate; Grinnell 1917, Kendeigh 1945). These vegetative and geographic characteristics are commonly used in habitat models for predicting a species' habitat across a landscape.

The usefulness of a habitat model depends on its predictive ability. Errors in predictions are generally attributed to data deficiencies, missing parameters, error introduced by specifications of the statistical model, and natural variation (Elith et al. 2002, Barry and Elith 2006, Guisan et al. 2006). Few researchers, however, have incorporated the influence of intra- and interspecific interactions (e.g., conspecific attraction, competition, predator–prey relationships) in habitat models. Interactions among organisms are likely to influence the distribution of species within available habitat by causing organisms to separate or cluster. Processes leading to individuals separating from one another include interspecific niche separation (MacArthur 1958) and negative density dependence (Fretwell and Lucas 1970, Rosenzweig 1991). Processes leading to clustering include conspecific attraction (e.g., Stamps 1988) and predator–prey relationships (e.g., Penteriani et al. 2006).

There is considerable literature documenting the clustered distribution of organisms within identified habitat (Allee 1927, Darling 1952, Post 1974, Stamps 1988, Hays and Lidicker 2000) and investigating mechanisms driving clustered distributions (reviewed by Hildén 1965), including public information (Doligez et al. 1999, 2004*a*, *b*) and prospecting (Ward 2005). A primary mechanism driving clustered distributions is conspecific attraction. Researchers have found through field and laboratory experiments that conspecific attraction explains clustered distributions for some species (Stamps 1988, Muller 1998, Poysa et al. 1998, Ward and Schlossberg 2004; reviewed by Ahlering and Faaborg 2006).

Conspecific attraction, or the tendency of individuals to be attracted to and, thus, settle near individuals of their own species can be caused by a variety of underlying mechanisms. Researchers have suggested several reasons that individuals may be attracted to conspecifics when selecting habitat, including more potential mates, group vigilance, predator dilution, and use of conspecifics as indicators of habitat quality (e.g., resource type and quality, previously successful breeding; summarized by Muller et al. 1997). Thus conspecific attraction can potentially lead to clustered

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distributions within identified habitat (reviewed by Reed and Dobson 1993).

We have found that few wildlife biologists have considered conspecific attraction leading to the clustered distribution of a species when building habitat models. Thus, our goals were to 1) review primary approaches to habitat modeling, focusing on associated prediction errors, 2) discuss conspecific attraction as it pertains to habitat selection, 3) outline the importance of considering conspecific attraction leading to clustered distributions in habitat modeling studies, 4) review examples where species clustering was considered in habitat models, and 5) provide preliminary considerations for sampling designs to investigate conspecific attraction. We provide a case study using golden-cheeked warblers (*Dendroica chrysoparia*) to illustrate the potential influence of conspecific attraction on habitat models.

Habitat Modeling And Prediction Errors

Habitat models are also referred to as niche-based models, species-distribution models, and biogeographical models of species distributions (Araújo and Guisan 2006, Guisan et al. 2006, Segurado et al. 2006). The process of creating a habitat model includes several steps. Wildlife biologists collect data at numerous locations, noting a species' presence or absence and measuring biotic and abiotic characteristics at each location. Often, the biotic and abiotic characteristics measured are those that are either noted with ease or assumed to affect occupancy, such as vegetative and geographic characteristics. Wildlife biologists then use a statistical model to select the characteristics that are significantly correlated with species occupancy (Araújo and Guisan 2006). Next, wildlife biologists use the specified vegetative and geographic characteristics to generate a spatially explicit prediction of the areas where a species is most likely to occur across a landscape (Barry and Elith 2006).

Incorrect predictions of presence–absence in habitat models are generally attributed to 1) data deficiencies, 2) missing parameters, 3) error introduced by the specifications of the statistical model, and 4) natural variation (Elith et al. 2002, Barry and Elith 2006, Guisan et al. 2006). Guisan et al. (2006) categorized data deficiencies as measurement errors and systematic errors. Measurement errors include missing variables, small sample sizes, biased samples, biased estimates of presence or absence, and a paucity of presence or absence data (e.g., species of interest was ubiquitous in sampled area; thus, characteristics of unoccupied habitat were not obtained). Systematic errors include datum shifts and misclassifications of vegetative cover in remote sensing data. Missing parameters are biotic and abiotic factors that might directly or indirectly influence a species occurrence, but are not included in the habitat model. Errors introduced by specifications of the statistical model, also referred to as model-based error, occur when statistical models with inappropriate probability distributions are used to create the habitat model (Guisan et al. 2006). Natural variation is stochasticity in ecological processes.

Recent improvements in habitat modeling have focused on correcting data deficiencies and statistical model-based errors. MacKenzie and Royle (2005) provided study design suggestions to account for detection probabilities that are <1 and to decrease some measurement errors caused by inappropriate sample sizes, biased estimates of occurrence, and biased samples. The development of improved statistical models has provided wildlife biologists with better tools to predict occurrence (Legendre 1993, Guisan et al. 2002, Lehmann et al. 2002). Statistical modeling developments include methods for identifying spatial autocorrelation (Legendre 1993, Augustin et al. 1998, Lichstein et al. 2002), methods for including spatial structures into statistical models (Legendre 1993), and advancements in regression analysis provided by generalized linear models and generalized additive models (Guisan et al. 2002, Lehmann et al. 2002). The least discussed type of error in habitat model predictions is natural variation. Predicting species occurrence requires a thorough understanding of the spatial and temporal changes in ecological interactions between the target species and their environment, including intra- and interspecific interactions (Leathwick and Austin 2001, Huston 2002, Guisan et al. 2006). Guisan et al. (2006) called for integrating ecological interactions into modeling species' distributions.

Conspecific Attraction

The presence of conspecifics may positively or negatively influence habitat selection. Conspecific competition influences habitat selection (Svardson 1949) through individual fitness declines with increasing density of conspecific competitors (Fretwell and Lucas 1970, Rosenzweig 1991). However, selecting habitat based on the presence of conspecifics may increase individual fitness (e.g., Ward 2005). Donohue (2006) described 2 classes of advantages yielded by association with conspecifics: positive density-dependent or Allee effects (Allee 1927) and use of conspecifics as indicators of habitat quality. Effects of positive density dependence can be seen in a reduced risk of predation (Bertness and Grosholz 1985, Ray and Stoner 1994, Tyler 1995), increased foraging success (Clark and Mangel 1984), and increased access to mates (Allee 1927). The information provided by the presence of conspecifics, termed public information, can reflect characteristics of habitat quality that may not be easily detectable or accessible to new settlers, such as resource abundance, predator densities, and potential for reproductive success (Danchin et al. 2001; Doligez et al. 2004*a, b*; Donahue 2006). Black-legged kittiwakes (*Rissa tridactyla*; Danchin et al. 1998), yellow-headed blackbirds (*Xanthocephalus xanthocephalus*; Ward 2005), and collared-flycatchers (*Ficedula albicollis*; Doligez et al. 1999, 2004*b*) selected habitat based on the previous reproductive success of neighboring conspecifics.

Conspecific attraction has been documented in laboratory experiments for several taxa including coral reef fishes (Sweatman 1985), the porcelain crab (*Petrolisthes cinctipes*; Donahue 2006), the sanddollar (*Dendraster excentricus*; Highsmith 1982), and Panamanian grass anoles (*Anolis* *auratus*; Kiester 1979). Conspecific attraction also has been observed in manipulative and mensurative field experiments for several taxa. Nest-box selection by naïve house wrens (*Troglodytes aedon*; i.e., individuals entering their first breeding season) was correlated with the presence of conspecifics (Muller et al. 1997). Muller (1998) found that habitat selection by a species of grasshopper (*Ligurotettix coquilletti*) was influenced by the presence of conspecifics. Similarly, conspecific attraction was found to influence habitat selection for mallards (*Anas platyrhynchos*; Poysa et al. 1998), pied flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1982), black-capped chickadees (*Peocile atricapillus*; Ramsay et al. 1999), and black-capped vireos (*Vireo atricapilla*; Ward and Schlossberg 2004). In some cases, individuals selected areas described as suboptimal habitat due to the influence of conspecific attraction (Tiainen et al. 1983). Conspecific attraction appears to influence habitat selection for a variety of species, which may cause spatial clustering of individuals.

Why Is Conspecific Attraction Important For Habitat Modeling?

Frequently, habitat models predict that a species will be present in certain areas, but some of those areas are not occupied. Likewise, species are found in some areas where the habitat model does not predict presence. These limitations in the predictive ability of habitat models are often attributed to missing habitat variables (Barry and Elith 2006). However, conspecific attraction leading to clustering of individuals within predicted habitat may explain the limitation of some habitat models (see Lichstein et al. 2002). Also, conspecific attraction may explain the presence of individuals outside of predicted habitat because individuals were attracted to the presence of conspecifics in adjacent areas of occupied, predicted habitat. Incorporating a parameter for clustering of individuals in habitat modeling can improve model predictions (Augustin et al. 1996, Lichstein et al. 2002).

Improving habitat models by incorporating a parameter for clustered distributions may provide more accurate predictions of a species' distribution and can assist wildlife managers by enabling them to focus on areas where occupancy is more likely. Improving a habitat model by incorporating such a parameter may reduce the search for missing vegetative and geographic parameters (Legendre 1993). Greater emphasis can then be placed on management, conservation, and investigating the mechanisms driving the clustered distribution of conspecifics within identified habitat, especially conspecific attraction.

Habitat Modeling For Clustered Distributions

Our review of the literature indicated that few wildlife biologists have considered clustered distributions of conspecifics in habitat models. However, statisticians and some wildlife biologists have used several statistical methods to address clustered distributions of conspecifics, beginning with agricultural pests and bacteria (Neyman 1939) and plants (Clark and Evans 1954). Logistic regression is commonly used to develop habitat models because wildlife survey data are typically treated as presence–absence (i.e., binomial) data.

We found 3 examples in the literature of statistical approaches to incorporate clustered distributions in habitat modeling. Smith (1994) used logistic regression with additional variables to explain and predict the spatial distribution of mountain sorrel (*Oxyria digyna*) in Britain. Smith (1994) assigned orders to adjacent cells to indicate their degree of proximity to a focal cell in a gridded sampling design and used the number of detections in each order of adjacent cells to generate the new variables. This method addressed autocorrelation in species distribution that could not be addressed by fitting other autocorrelated environmental variables associated with occurrence. Smith (1994) found that incorporating the additional variables improved both the explanatory and predictive capabilities of the habitat model. Augustin et al. (1996, 1998) created a habitat model to predict red deer (*Cervus elaphus*) distribution in Scotland using a gridded sampling design. Augustin et al. (1996, 1998) analyzed survey data by extending a logistic regression model to incorporate a parameter indicating presence–absence at neighboring survey locations to account for autocorrelation in red deer distributions. Augustin et al. (1996) found that including this parameter significantly improved their estimate of the spatial distribution of red deer across the landscape compared to a logistic-regression model without the added parameter. Cornulier and Bretagnolle (2006) used point-process statistics to test for the clustered distribution of nests with respect to available habitat for little owl (*Athene noctua*) and Montagu's harrier (*Circus pygargus*) in France. Cornulier and Bretagnolle (2006) suggested using point-process statistics (the $K(r)$ function [see Ripley 1977]) to analyze data consisting of point locations within a defined area to detect interactions in the point pattern such as aggregation or inhibition. Cornulier and Brentagnolle (2006) found that observing aggregation depended on the spatial scale considered and on accounting for available habitat for each species.

These examples demonstrate several methods of incorporating metrics that reflect clustered distributions, and that such approaches can improve the predictive ability of habitat models. These habitat modeling methods seem especially applicable to management and conservation of wildlife because they extrapolate sample data to predict a species' distribution across a landscape.

Sampling For Conspecific Attraction

To our knowledge, few field experiments have used sampling designs to explicitly evaluate the occurrence of conspecific attraction across large spatial scales and its influence on a species' distribution. Wildlife biologists have used manipulative experiments in the lab (e.g., Kiester 1979, Sweatman 1985, Donahue 2006) and field (Muller 1998, Ward and Schlossberg 2004, Ahlering and Faaborg 2006) to determine if species respond to conspecific cues (e.g., presence of conspecifics, visual models, vocalizations). Also, research has focused on correlating territory or nest-site selection with the presence of conspecifics on relatively small spatial scales (e.g., Tiainen et al. 1983, Muller et al. 1997, Doligez et al. 1999). Conspecific attraction is likely to influence a species' distribution on both small and large spatial scales; thus, sampling for conspecific attraction should be incorporated into occupancy studies.

Estimates of abundance or occupancy are usually based on designs where sampling is conducted on an annual basis (e.g., winter surveys for ungulates). Thus, these estimates are influenced primarily by sampling variation (e.g., variability among counts, variability among plots). Most studies focus little effort on quantifying process variation, primarily based on the assumption that organisms at the plot level are affected equally by changes in environment or demographic process. Sampling designs for conspecific attraction must account for temporal and spatial variation because these factors are inherent to conspecific attraction. Depending on the reproductive phenology of the study species, conspecific attraction may occur in one week or occur irregularly across a season (temporal variation). Also, conspecific attraction may occur on small or large spatial scales both within and among habitat patches (spatial variation).

Many sampling designs are potentially useful for evaluating conspecific attraction in wildlife species, including multistage sampling (Thompson 2002), ranked-set sampling (Thompson et al. 1998), double-sampling (Bart and Earnst 2002), or adaptive sampling (Thompson and Seber 1996, Thompson 2002). Sampling designs developed for clustered populations are focused primarily on incorporating clustering into survey plots, often with the benefit of reduced variance and increasing estimator precision (Thompson and Seber 1996, Thompson 2002). Plot delineation for evaluation of conspecific attraction is difficult, especially in the case of breeding birds. Vegetative and geographic metrics are frequently used to determine plot size, shape, and placement (Morrison et al. 2001). However, multiple patches of high-quality habitat may exist within a woodland, wetland, or meadow. Development and application of designs to differentiate between clustering due to conspecific attraction and clustering due to the clustering of other habitat characteristics (e.g., resources, vegetation structure) should become an active area of research in habitat modeling.

A Case For Conspecific Attraction In Golden-Cheeked Warblers

Wildlife biologists have described golden-cheeked warbler habitat as mature oak–juniper (*Quercus–Juniperus*) woodland (Pulich 1976, Kroll 1980, Ladd and Gass 1999, Magness et al. 2006). Researchers have used habitat models to predict golden-cheeked warbler occupancy using parameters associated with mature oak–juniper woodland (Cummins 2006, DeBoer and Diamond 2006, Jones 2006). Prediction errors of the habitat models were attributed to data deficiencies (e.g., small sample size, inability to detect fine distinctions in habitat parameters) and missing habitat parameters (e.g., woodland stand age, habitat structure, regional variability in warbler habitat; DeBoer and Diamond 2006) or the errors were not addressed (Cummins 2006, Jones 2006). Conspecific attraction was not considered in these habitat models for golden-cheeked warblers.

Based on the previous research noted above, we created a habitat model using a Landsat map of east-central Texas, USA, prepared by the University of Texas at Austin Center for Space Research. University of Texas at Austin Center for Space Research used sub-pixel classification to identify the vegetation species in each pixel of the Landsat map. We used an ArcGIS™ Spatial Analyst Neighborhood Statistics procedure with a 400-m radius moving window on the classified map to identify areas with <40%, 40–60%, and >60% oak–juniper woodland composition. We based these composition classes on research showing that golden-cheeked warblers were increasingly likely to occupy areas with greater percentage oak–juniper woodland composition (Cummins 2006, DeBoer and Diamond 2006) and were unlikely to occupy areas with oak–juniper woodland composition <40% (Magness et al. 2006).

We conducted 6 point-count surveys from 1 April to 1 June 2006 at 211 survey stations. We used these data to evaluate the predictive ability of our habitat model for predicting golden-cheeked warbler occurrence. We detected golden-cheeked warblers at 20% of point-count stations in <40% oak–juniper woodland ($n = 127$), 62% of stations in 40–60% ($n = 53$), and 84% of stations in >60% ($n = 31$). We detected warblers in some areas where the habitat model did not predict occupancy (<40% oak–juniper woodland) and did not in some areas where the habitat model predicted occupancy (>60% oak–juniper woodland).

We examined our data for evidence of conspecific attraction to potentially explain errors in the predictive ability of the habitat model. Our objective was to determine if a warbler detection in a higher oak–juniper composition class would increase the probability of a detection in a neighboring, lower oak–juniper composition class. For each point-count station where we detected a warbler, we calculated the proportion of point-count stations both within 400 m and in lower percent oak–juniper composition where we also detected warblers. For each point-count station where we did not detect a warbler we calculated the proportion of point-count stations both within 400 m and in lower percentage oak–juniper composition where we detected warblers.

Forty-one point-count stations met our criteria having neighboring points both within 400 m and in lower oak–juniper composition classes. For stations where we detected a warbler, the proportion of adjacent stations in a lower composition class that were occupied was 0.64 (SE = 0.01, median = 0.50, mode = 1, $n = 27$). For stations where we did not detect a warbler, the proportion of adjacent stations in a lower composition class that were occupied was 0.48 (SE = 0.03, median = 0.24, mode = 0, $n = 14$). The difference between these proportions was 0.16 (95% CI = –0.16–0.48). Although this interval was not statistically different, it contained differences we suggest may be biologically important for understanding the distribution of golden-cheeked warblers.

Our preliminary analysis found that warblers were more likely to be present in a lower composition class if there was a warbler present in an adjacent higher composition class and we suspect this may be due to conspecific attraction. Our findings suggest that the presence or absence of conspecifics in adjacent areas influences the distribution of golden-cheeked warblers within mature oak–juniper woodland. We collected our occupancy data as part of a larger monitoring project that was not explicitly designed to investigate conspecific attraction or clustered distributions and may need to be adjusted to more rigorously pursue this objective. Future research is needed to determine if golden-cheeked warblers are clustered within available habitat. If clustered distributions are observed, future research is needed to determine if conspecific attraction is a mechanism driving clustered distributions.

Management Implications

We urge wildlife biologists to consider conspecific attraction and the resulting clustered distributions in their habitat models to explain and predict species occurrence across a landscape. We expect that habitat models incorporating a parameter for clustered distributions will have improved predictive ability and, thus, become more useful tools for management and conservation efforts.

Information on conspecific attraction leading to clustering can influence management needs and objectives for wildlife species. The management objective may be to conserve or restore all potentially suitable habitat for a species of interest. In this case, we recommend creating habitat models with and without a parameter for clustered distributions. The habitat model without a clustering parameter is likely to identify all areas with the specified vegetative and geographic characteristics thought to be suitable for the species. The habitat model with a parameter for clustered distributions can be used to determine if the species of interest is indeed clustered within areas identified by the habitat model constructed with vegetative and geographic parameters only. If clustering is observed, the absence of the species in areas predicted to be suitable based on vegetative and geographic parameters may not be due to unsuitability of these characteristics, but to inter- and intraspecific interactions, especially conspecific attraction. This information on clustered distributions can be used to support management actions to conserve and restore currently unoccupied habitat. Especially in the case of endangered species, there may not be enough individuals to occupy all potential habitat, and to recover a species, potential habitat that is currently unoccupied will need to be occupied in the future.

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LITERATURE CITED

Ahlering, M. A., and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk 123:301–312.

Alatalo, R. V., A. Lundberg, and M. Bjorklund. 1982. Can the song of male birds attract other males? An experiment with the pied flycatcher (*Ficedula hypoluca*). Bird Behaviour 4:42–45.

Allee, W. C. 1927. Animal aggregations. The Quarterly Review of Biology 2:367–398.

Araújo, M. B., and A Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.

Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33:339–347.

Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1998. The role of simulation in modeling spatially correlated data. Envirometrics 9:175–196.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43:413–423.

Bart, J., and S. Earnst. 2002. Double-sampling to estimate density and population trends in birds. Auk 119:36–45.

Bertness, M. D., and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. Oecologia 67:192–204.

Clark, C. W., and M. Mangel. 1984. Foraging and flocking strategies: information in an uncertain environment. American Naturalist 123:626–641.

Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

Cornulier, T., and V. Bretagnolle. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. Ecography 29:240–250.

Cummins, T. 2006. The use of GIS and remotely sensed data in predicting the occurrence of two endangered avian species in central Texas. Thesis, Texas A&M University, College Station, USA.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Danchin, E., D. Heg, and B. Doligez. 2001. Public information and breeding habitat selection. Pages 243–258 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford, United Kingdom.

Darling, F. F. 1952. Social behavior and survival. Auk 69:183–191.

DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence–absence of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). Southwestern Naturalist 541:181–190.

Doligez, B., E. Danchin, J. Clobert, and L. Gustaffson. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology 68:1193–1206.

Doligez, B., T. Part, and E. Danchin. 2004*a*. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Animal Behaviour 67:457–466.

Doligez, B., T. Part, E. Danchin, J. Clobert, and L. Gustaffson. 2004*b*. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. Journal of Animal Ecology 73:75–87.

Donahue, M. J. 2006. Allee effects and conspecific cueing jointly lead to conspecific attraction. Oecologia 149:33–43.

Elith, J., M. A. Burgman, and H. M. Regan. 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. Ecological Modelling 157:313–329.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Theoretical development. Acta Biotheoretica 19:16–36.

Grinnell, J. 1917. Field tests of theories concerning distributional control. American Naturalist 51:115–128.

Guisan, A., J. Edwards, C. Thomas, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89–100.

Guisan, A. J., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall, and T. Hastie. 2006. Making better biogeographical predictions of species' distributions. Journal of Applied Ecology 43:386–392.

Hays, W. S. T., and W. Z. Lidicker, Jr. 2000. Winter aggregations, Dehnel effect, and habitat relations in the Suisun shrew (*Sorex ornatus sinuosus*). Acta Theriologica 45:433–442.

Highsmith, R. C. 1982. Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free adult sand dollar beds. Ecology 63:329–337.

Hildén, O. 1965. Habitat selection in birds. Annales Zoologici Fennici. 2: 53–75.

Huston, M. A. 2002. Introductory essay: critical issues for improving predictions. Pages 7–21 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California, USA.

Jones, J. S. 2006. Development of a decision support geographic information system for land restoration programs in the Leon, Lampasas, and Bosque river watersheds. Thesis, Texas A&M University, College Station, USA.

Kendeigh, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk 62:418–436.

Kiester, A. R. 1979. Conspecifics as cues: a mechanism for habitat selection in the Panamanian grass anole (*Anolis auratus*). Behavioral Ecology and Sociobiology 5:323–330.

Kroll, J. C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. Journal of Range Management 33:60–65.

Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). Account 420 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Leathwick, J. R., and M. P. Austin. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. Ecology 82:2560–2573.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Lehmann, A., J. M. Overton, and M. P. Austin. 2002. Regression models for spatial prediction: their role for biodiversity and conservation. Biodiversity and Conservation 11:2085–2092.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72:445–463.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42: 1105–1114.

Magness, D. R., R. N. Wilkins, and S. J. Hejl. 2006. Quantitative relationships among golden-cheeked warbler occurrence and landscape size, composition, and structure. Wildlife Society Bulletin 34:473–479.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, New York, New York, USA.

Morrison, M. L., W. M. Block, M. Dale Strickland, and W. L. Kendall. 2001. Wildlife study design. Springer-Verlag, New York, New York, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. Wildlife–habitat relationships. Third edition. Island Press, Washington, D.C., USA.

Mörtberg, U., and A. Karlström. 2005. Predicting forest grouse distribution taking account of spatial autocorrelation. Journal of Nature Conservation 13:147–159.

Muller, K. L. 1998. The role of conspecifics in habitat settlement in a territorial grasshopper. Animal Behaviour 56:479–485.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150:650–661.

Neyman, J. 1939. On a new class of "contagious" distributions, applicable in entomology and bacteriology. Annals of Mathematical Statistics 10: 35–57.

Penteriani, V., M. A. Fortuna, C. J. Milian, F. Otalora, and M. Ferrrer. 2006. Can prey behaviour induce spatially synchronic aggregation of solitary predators? Oikos 113:497–505.

Post, W. 1974. Functional analysis of space-related behavior in the seaside sparrow. Ecology 55:564–575.

Poysa, H., J. Elmberg, K. Sjoberg, and P. Nummi. 1998. Habitat selection rules in breeding mallards (*Anas platyrhynchos*): a test of two competing hypotheses. Oecologia 114:283–287.

Pulich, W. M. 1976. The golden-cheeked warbler, a bioecological study. Texas Parks and Wildlife Department, Austin, USA.

Ramsay, S. M., K. Otter, and L. M. Ratcliffe. 1999. Nest site selection by female black-capped chickadees: settlement based on conspecific attraction? Auk 116:604–617.

Ray, M., and A. W. Stoner. 1994. Experimental analysis of growth and survivorship in a marine gastropod aggregation: balancing growth with safety in numbers. Marine Ecology Progress Series 105:47–59.

Reed, A. M., and A. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends in Ecology and Evolution 8:253–256.

Ripley, B. D. 1977. Modelling spatial patterns. Journal of the Royal Statistical Society B39:172–212.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137:S5–S28.

Segurado, P., M. B. Araújo, and W. E. Kunin. 2006. Consequences of spatial autocorrelation for niche-based models. Journal of Applied Ecology 43:433–444.

Smith, P. A. 1994. Autocorrelation in logistic regression modelling of species' distributions. Global Ecology and Biogeography Letters 4:47–61.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist 131:329–347.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1: 157–174.

Sweatman, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. Ecological monographs 55:469–485.

Thompson, S. K. 2002. Sampling. Second edition. John Wiley and Sons, New York, New York, USA.

Thompson, S. K., and G. A. G. Seber. 1996. Adaptive sampling. John Wiley and Sons, New York, New York, USA.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California, USA.

Tiainen, J., M. Vickholm, T. Pakkala, J. Piiroinen, and E. Virolainen. 1983. The habitat and spatial relations of breeding *Phylloscopus* warblers and the goldcrest *Regulus regulus* in southern Finland. Annales Zoologica Fennici 20:1–12.

Tyler, W. A. I. 1995. The adaptive significance of colonial nesting in a coral-reef fish. Animal Behaviour 49:949–966.

Ward, M. P. 2005. Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. Oecologia 145:650–657.

Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519–525.